ECOLOGY AND FUNCTIONAL MORPHOLOGY OF AN UNCINULID BRACHIOPOD FROM THE DEVONIAN OF SPAIN

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ABSTRACT. The orientations, with respect to the bedding-planes, of 145 specimens of *Uncinulus pila* (Schnur, 1851) were plotted. From the results it is concluded that this species lived with its beak downwards and that the posterior region, in the sediment, was sealed by squamae and glottae. This interpretation is supported by the mesothyridid to permesothyridid pedicle opening. This life position would have been advantageous in helping the separation of inward and outward currents of sea-water, especially if the animal could rotate on its pedicle in response to changes in the marine flow. Geniculation, at the end of the brephic stage of ontogeny, involved important alterations in the life habits of *U. pila*; in particular its orientation changed from resting on its dorsal valve to the adult vertical position. The ecology of related species is compared and the convergence of habit of the Permian tetracamerid *Septacamera* is noted.

UNCINULIDAE are a group of rhynchonellid brachiopods which are a characteristic constituent of many Silurian and Devonian rocks. Their morphology is eminently suitable for functional, ontogenetic, and phylogenetic analysis and has already been the subject of a number of more or less detailed investigations (Schmidt 1937; Schumann 1965; Westbroek 1967). Fieldwork in the Cantabrian Mountains in Spain has allowed us to study the position of shells of one species of this family, *Uncinulus pila* (Schnur, 1851) in the surrounding rock. These observations, together with some new morphological data, led to reconstruction of the life habits of this species. Moreover, the ecological interpretation allows a better understanding of its morphology and, to a lesser extent, of its ontogeny. On morphological grounds it is suggested that the life habits of *U. pila* were operative in a major part of the family.

MATERIALS AND TECHNIQUES

In total 145 specimens of *U. pila* were collected at four different localities (text-fig. 1) in the Lavid Formation of the Southern Cantabrian Mountains (Emsian, province of León, Spain). On each specimen the orientation relative to the bedding-plane was marked. The angles between both the plane of symmetry of the shell and the interpolated 'horizontal plane' (between both valves) and the bedding-plane were then determined with the Ingerson apparatus (Ingerson 1941). The intersection of the plane of symmetry and the horizontal plane is called here the *longitudinal axis*. The orientation of the shell relative to the bedding-plane could now be plotted on a Wulff's net. With the aid of a counting net (Kalsbeek 1963) a representation of the distribution of the projections on the Wulff's net could be obtained. Plots of the few shells where the antero-posterior direction of the longitudinal axis (and thus the umbo) pointed upwards were not taken into consideration.

For morphological studies of the internal structure of *U. pila*, internal moulds
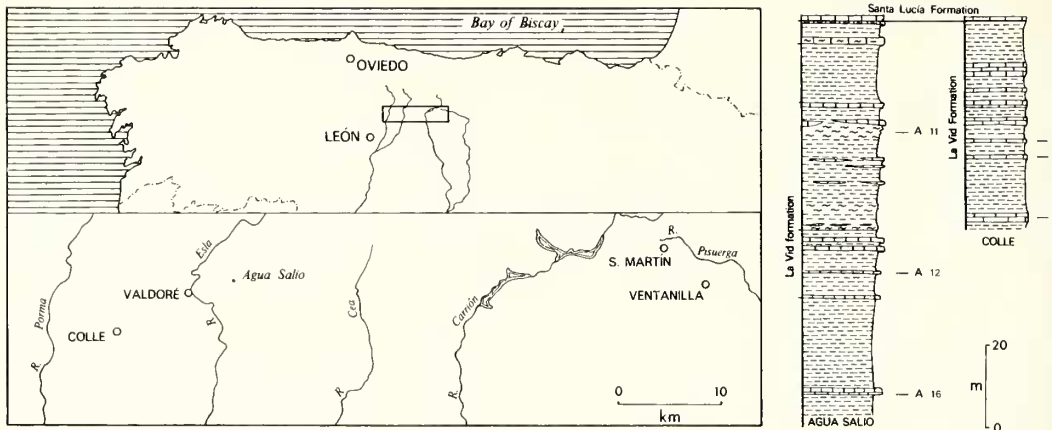
TEXT-FIG. 1. Collection localities for *Uncinulus pila*; 84 specimens from Colle; 61 specimens from Aguasalio. The internal mould figured (Pl. 51, fig. 3) is from between S. Martín and Ventanilla.

were used which were collected at a locality between Ventanilla and San Martín de los Herreros, described by Kanis (1956, pp. 390 and 392, fig. 10 and appendix 3, section II) (see text-fig. 1).

OBSERVATIONS

The ontogeny of all uncinulids characteristically proceeds in two stages (text-fig. 2): brephic shells are flat and grow mainly in length and width. By the end of the brephic stage both valves suddenly start growing in opposite directions so that they make an angle of 180° or even slightly more all along the commissure. As a result of this geniculation a vertical wall is formed and the shell grows in thickness. Geniculation is functionally related with the development of marginal spines—elongated out-growths of the grooves between the costae—along both valve margins, forming a highly protective grill when the shell is opened. Since the spines project inside the mantle cavity just behind the opposite valve they can only be formed in a geniculated shell. Hence, this protective device can only develop in the post-brephic stage; it is absent in the brephic shell. No spines are formed in the most posterior parts of the geniculated region. In the more evolved uncinulids, like *U. pila*, a squama and a glotta are formed which close off the gape at these sites when the shell is opened (text-fig. 4; Pl. 51, figs. 1*b*, 2*b*).

Uncinulids are uniplicate, i.e. the commissure displays a broad median deflection in the dorsal direction. By analogy with the recent rhynchonellide *Notosaria* it is suggested that this deflection served to separate lateral inward streams of sea-water into the mantle cavity from the median outward stream of filtered water into the sea. Thus the commissure can be divided into five functionally different parts: postero-laterally the shell is sealed off by a pair of squamae and glottae; the inhalant apertures are situated (antero)laterally and the exhalant aperture anteriorly and medially. In most uncinulids, especially in *U. pila*, this functional five-fold subdivision of the commissure is further accentuated by the subpentagonal outline of the shell in dorsal

brephic shell

geniculated
region

post–brephic shell
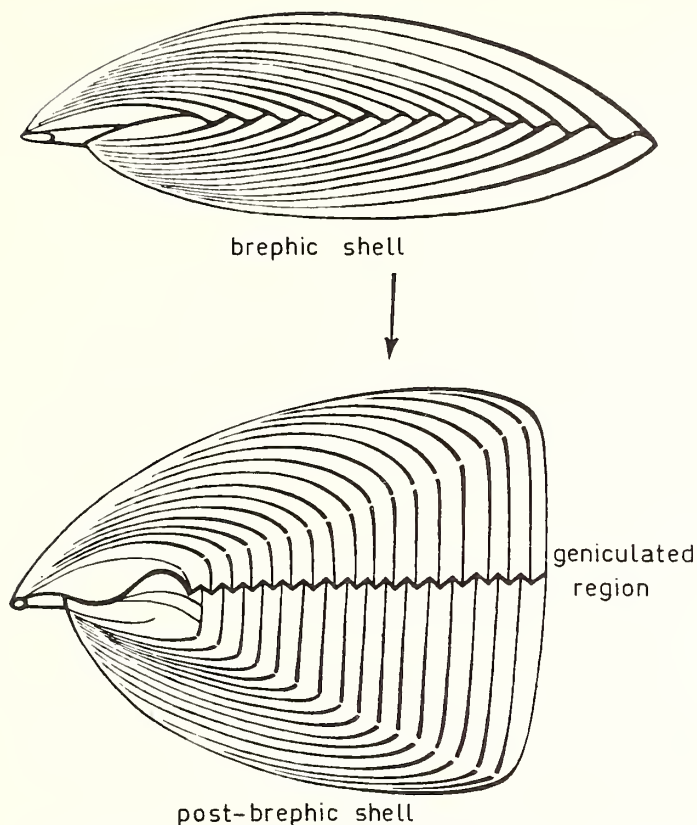
TEXT-FIG. 2. Geniculation in uncinulid brachiopods and explanation
of terminology.

and ventral view (Pl. 51, fig. 1*a*, *b*, *c*). The postero-lateral sides make an obtuse angle,
thus giving the shell a stumpy appearance. Along this part of the commissure the
gape was closed off by the squamae and glottae which extend precisely from the hinge
to the junction with the lateral sides. The lateral sides are subparallel; anteriorly they
bend in median direction. Their transition with the postero-lateral sides is not sharply
defined but their passage towards the median side which corresponds with the median
deflection of the commissure and thus with the exhalant part of the gape, is marked
by a sharp vertical ridge. In most of the specimens of *U. pila* the median deflection of
the commissure has also a marked posteriorly directed component throughout the
ontogeny. As a result the sulcus extends smoothly from near the ventral umbo to the
dorsal geniculation. This combination of factors must have provided a neat separa-
tion of the inward stream of sea-water (in postero-median direction) from the out-
ward stream (antero-medially). Later on it will be shown how the median trough may
have funnelled currents in the surrounding sea-water, so that a maximum separation
of inwardly and outwardly streaming water was achieved.

The delthyrium is largely sealed off by a deltidium and the position of the pedicle
opening is mesothyridid to permesothyridid, i.e. the very tip of the ventral valve is

dissolved between the dental plates, leaving an elongate slot through which the pedicle could protrude (Pl. 51, fig. 2a, b). This tiny slot and the deltidium is only visible in very few specimens due to abrasion of the fragile umbo. In an earlier study it was tacitly assumed that no such foramen and deltidial plates would occur in species related to *U. pila* (e.g. Westbroek 1967, fig. 53). But at that time these structures were only considered from a static and not from a dynamical and functional point of view. A dynamical approach to fossils sharpens the eye for structural observation. Plate 51, fig. 3a, b shows a typical internal mould of *U. pila* in ventral view. The position of the ventral adjustor scars could not be determined with certainty on the available moulds. The posterior end of the shell, especially of the ventral valve, is very massive, as suggested by the deep excavations of the mould. But the mould shows a strongly jutting knob in the very umbonal part of the ventral valve, between the dental plates. Here, a well-developed pedicle capsule has been accommodated. A sharp transverse line across the knob probably belongs to a scar of the 'median adjustor'. The location of the pedicle capsule and of the foramen suggests that the preferential direction of the pedicle was antero-posterior.

Text-fig. 3 shows the distribution of the orientation of the shells relative to the bedding-plane in the different localities where samples were taken. Also, the distribution of the total number of specimens from Aguasalio and Colle together are given (text-fig. 3d). From these graphs it is evident that a large percentage is lying on the pedicle valve (53 specimens, i.e. 37% of the total), and a somewhat lesser percentage on the brachial (20 specimens, 14% of the total). Only 13 shells out of the total of 145 (9%) were lying upside down, i.e. the antero-posteriorly directed 'longitudinal axis' (see above), and thus the umbo, pointed upwards. These shells were not considered in the interpretation of the life position of the animals. Of the 145 shells 54 (37%) were oriented otherwise, and in 26 out of these (18%), the longitudinal axis made an angle of 60° or more with the bedding-plane. The distribution charts display a rather narrow elongated zone from a dorsal, via a vertical, towards a ventral orientation with a marked maximum round a vertical position and minima close to the ventral and dorsal orientations.

In the localities where the sampling was carried out *U. pila* occurs in shaly marls containing abundant fossils and fragments of fossils. At the moment of deposition the sediment must have been a soft mud with many poorly sorted bioclasts. *U. pila* could well be partly buried in the mud and also could adhere with its pedicle to the bioclasts, so that its position was stabilized.


EXPLANATION OF PLATE 51

Figs. 1–3. *Uncinulus pila.* 1a–c, ventral, lateral, and frontal views of specimen from Colle, ×4. a, shows the subpentagonal outline of the shell; b, c, relate the uniplicate nature of the commissure with the shape of the shell. A squama is visible in b. 2a, b, morphology of the umbo in two specimens from Aguasalio. The meso- to permesothyridid foramina, the deltidial plates, and a squama are visible. a, ×9; b, ×7. 3a, b, internal mould of a ventral valve, collected between San Martin and Ventanilla. Note the jutting knob in the very umbonal part of the valve, very probably corresponding with a well-developed pedicle capsule. ×4·5.

All specimens in Department of Stratigraphy and Palaeontology, Geological Institute, State University, Leiden. Fig. 1a–c, W 001; fig. 2a, W 002; fig. 2b, W 003; fig. 3a, b, W 004.

PLATE 51
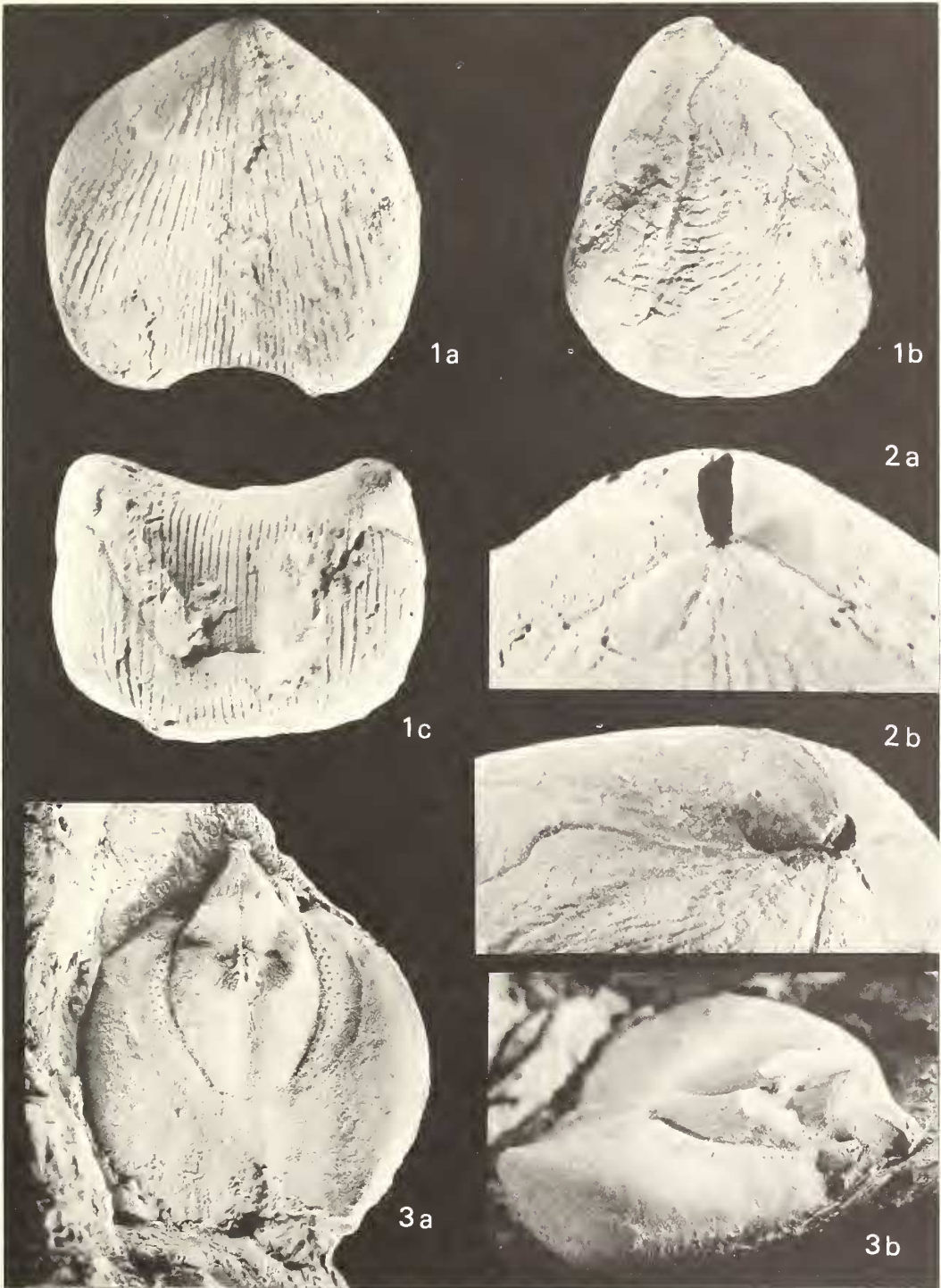
WESTBROEK, NEIJNDORFF and STEL, *Uncinulus pila*
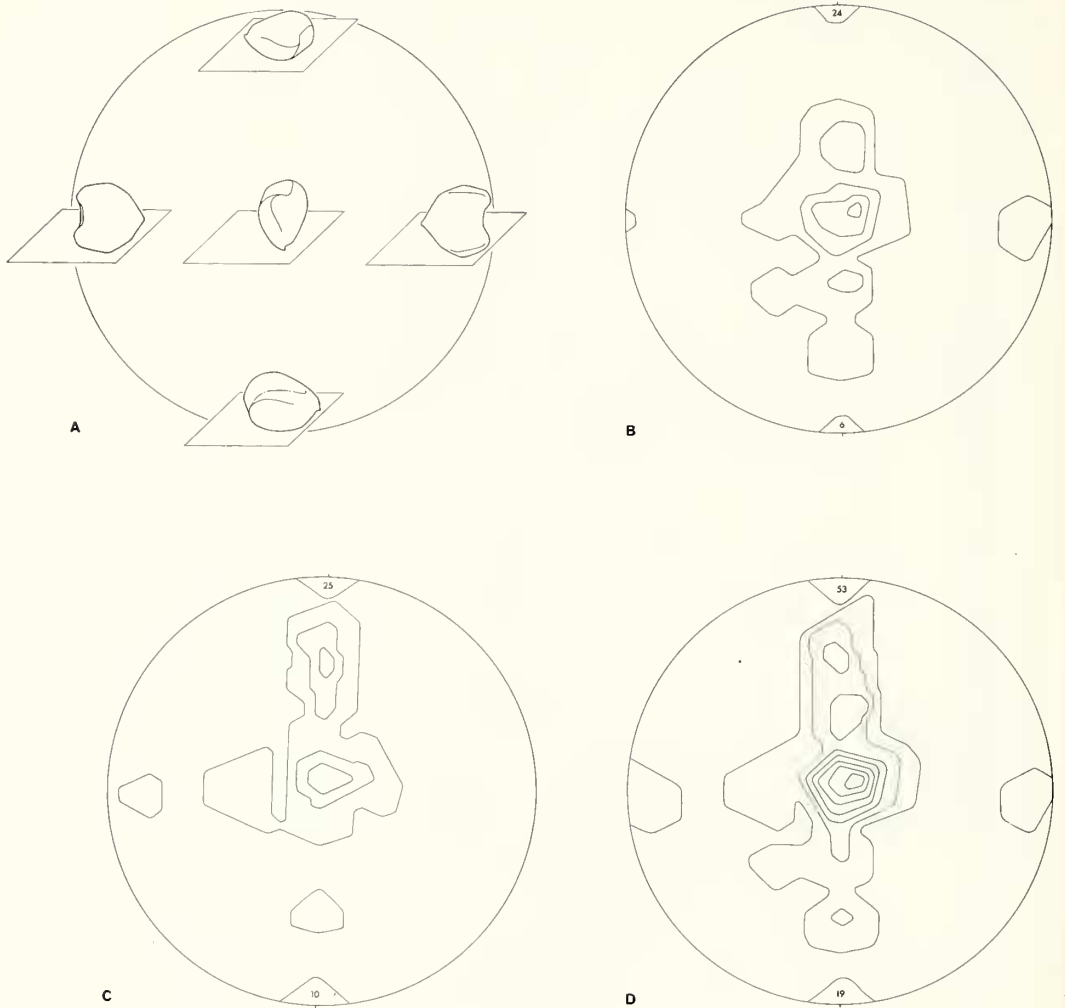
TEXT-FIG. 3. Orientation of shells with respect to the bedding-plane. The lines on the charts connect points where the number of specimens exceeds the values of 1, 3, 5, 7, 9, 11, and 13 per 1% of the total area per chart. For plotting procedure see 'Materials and Techniques'.

A, shows with five examples how the location on the charts must be interpreted with respect to shell orientation.

B, distribution of the orientations of the 61 specimens collected in Aguasalio.

C, distribution of the orientations of the 84 specimens collected in Colle.

D, distribution of the orientations of the 145 specimens collected in Aguasalio and Colle together.

CONCLUSIONS

To judge from the shell shape most transported shells will have ended up lying either on the dorsal or on the ventral valve. The most unlikely position would be with the beak downwards. This would be like a top standing on its sharp point without spinning. The pronounced maximum for shells in exactly this position (text-fig. 3) is, therefore, taken to represent specimens in life position. The shells which lie on the valve surfaces are assumed to be transported by streaming water or otherwise. The elongation of the maximum towards the ventral and dorsal positions may be due to incipient post-mortem transport, but it is also possible that this represents *in vivo* deviations from the normal vertical position. Possibly the animals were able to tilt their shells and so to adapt themselves to water currents and other conditions. The fact that so many shells have been preserved in so unlikely a position is considered here as an indication that after death they were kept in place by the surrounding sediment: they must have been partly buried in the mud. Most probably the posterior part of the shell, including the strongly diverging postero-lateral sides of the geniculated region, was stuck in the sediment. This part of the commissure was permanently sealed off from the surrounding medium by the squamae and glottae; the subparallel lateral parts of the commissure could then accommodate the inward stream of seawater. The posterior part of the shell is often strongly thickened and the corresponding shift of the centre of gravity towards the umbo will have helped to keep the shell in this position.

The aforementioned antero-posterior orientation of the pedicle fits in this interpretation remarkably well. Probably the slender pedicle was root-like and adhered to relatively large particles in the sediment, or, in their absence, protruded deep enough into the soft mud to maintain the animal's position and to allow organized reorientations.

By adjusting its position with respect to water currents the animal would have been able to separate the inward and outward water streams most efficiently, as is evident from text-fig. 4. Moreover, the smooth and trough-like sulcus would have smartly funnelled the water stream, thus removing the waste water as efficiently as possible.

The process of geniculation which marks the end of the brephic stage, must have been a complete and sudden reversal in the entire organization of the animal. Apart from a radical change in the direction of shell growth along the valve margins it involved the formation of the marginal spines as a highly effective protective device and a sudden increase in height instead of in width of the spiroloph (Westbroek 1967, p. 36). Weak postero-lateral costae which die out against the squamae and glottae (Westbroek 1967, p. 50) indicate that in brephic individuals the posterior parts of the commissure were not sealed off, so that these young animals cannot have been buried in the sediment with their posterior ends; they must have lived on the dorsal valve instead. So, together with geniculation, a drastic alteration of the animal's orientation must have taken place. It is likely that the orientation of the pedicle was changed accordingly and that the pedicle opening was modified from hypothyridid to submesothyridid by resorption of the tip of the ventral valve between the dental plates.

If our interpretation concerning the life position of *Uncinulus pila* and the correlation with the morphology of the shell is correct, then the presence of squamae and

glotta

squama
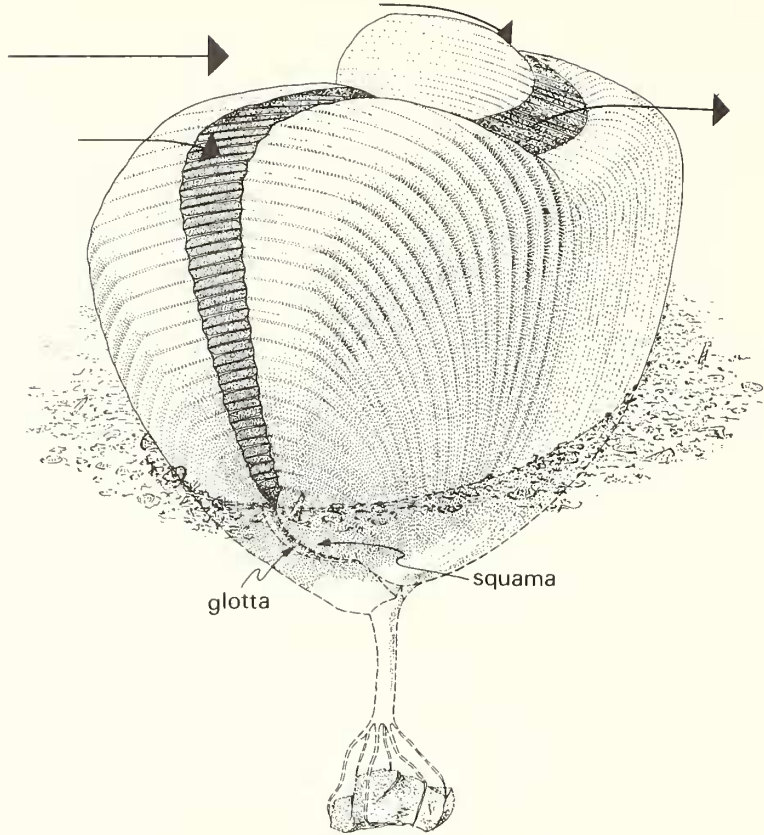
TEXT-FIG. 4. Interpretation of the life-habits of *Uncinulus pila*.

glottae and a posteriorly directed pedicle opening in other related species may indicate in themselves a similar ecology. In the framework of this publication it was not possible to inspect these characters in more than a few related species. Both *U. subwilsoni* (d'Orbigny, 1850) from the Siegenian Lebanza Formation (Binnekamp 1965), and *U. orbignyanus* (de Verneuil, 1850) from the Eifelian Santalucía Formation are very much like *U. pila* in so far as these relevant characters are concerned. Thus, very probably all three species have behaved similarly with respect to the substratum. The upper Wenlock to Ludlow *Sphaerirhynchia wilsoni* (Sowerby, 1816) which may be regarded as the ancestor of *Uncinulus* (Westbroek, 1967) is remarkably different. Here the posterior part of the gape was not sealed off by squamae and glottae and the position of the pedicle opening was hypothyridid to submesothyridid. Consequently, the shell was probably lying on the dorsal valve and the umbonal part was not buried in the substratum. Thus, this primitive uncinulid behaved like a brephic *Uncinulus* in so far as the orientation of its shell is concerned.

The Permian tetracamerid *Septacamera* Stepanov is a remarkable case of convergence. Grant (1971) described the morphology and the ecology of representatives of this genus. The shell is geniculated and pronounced marginal spines are developed.

The posterior part of the gape was permanently sealed off. The orientation of the shell was vertical and it was maintained in this position by a stout pedicle which protruded through a permesothyridid opening. Unlike *U. pila* the umbo was buried only occasionally. Those widely unrelated taxa must have produced the same morphology and life habits through independent processes of mutation and selection.

The orientation of the fossils in the bedding-plane has been used here as an argument in the ecological interpretation. However, once the vertical life-position of *Uncinulus* is accepted, measurements of the orientation of shells of this genus can be used to estimate post-mortem disturbances of the environment. We estimate, however, that more information must be gathered from other localities and from other species, before the argument can be reversed in this sense into a reliable palaeo-ecological tool.

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